ENTEROPNEUSTA

BY

ETHELWYNN TREWAVAS, B.Sc.

WITH EIGHTEEN TEXT-FIGURES.

INTRODUCTION.

The Enteropneusta are represented in the collections of the Great Barrier Reef Expedition by adults of two species and Tornaria larvae of at least seven species.

The adults are *Ptychodera flava*, Eschscholtz, and *Balanoglossus carnosus* (Willey), both members of the family Ptychoderidae. Both have a wide Indo-Pacific distribution, and each has a closely related species in the West Indies. *Ptychodera flava* has been

recorded from Sydney, New South Wales, and an identical or closely related species is known from the Abrolhos Islands, off Western Australia ; but this is the first record of *Balanoglossus carnosus* from the Australian coast.

None of the Tornariae can be matched with its adult, and the elucidation of the life-histories of the Pacific Enteropneusta is a much-needed piece of work. Four species are here described as new ; one of these is represented by fifty-nine specimens, but none of the others is described from more than five individuals.

Here I gladly express my gratitude to Miss A. B. Hastings, B.A., Ph.D., and to Capt. A. K. Totton, M.C., who separated some of these larvae from the plankton samples for me, while searching for members of other groups.

I am indebted to the Zoological Museum of the University of Cambridge for the loan of " cotypes " (? syntypes) of *Ptychodera asymmetrica*, Punnett, *Pt. viridis*, Punnett, and of the varieties of *Pt. flava* described by Punnett from the Maldives and Laccadives (except var. *muscula*). In addition, I have had for comparison syntypes of *Balanoglossus carnosus* (Willey), specimens of *Ptychodera flava*, collected and described by Willey, from New Caledonia, and a specimen of *Pt. bahamensis*, Spengel. These are in the collection of the British Museum (Natural History).

PTYCHODERA FLAVA, ESCHSCHOLTZ.

Ptychodera flava, Eschscholtz,* 1825, p. 740, pl. v, fig. 8. Spengel, 1893, p. 190, fig. p. Hill, 1897, p. 205. Willey, 1897, p. 165, pl. v ; 1899, p. 227, pls. xxvi, xxviii, figs. 1*a*, 2–11, pl. xxix, figs. 12–15, pl. xxxii, figs. 66–68. Punnett, 1903, p. 644, pls. xxxvii–xl, xlii–xlvi. Spengel, 1903, p. 271, pls. xxiv–xxix ; 1904*a*, p. 1, pl. i. Van der Horst, 1930, p. 195, figs. 62–64.

? *Balanoglossus tricollaris*, Schmarda, 1871–2, p. 273,† fig. (2nd edit. 1877, p. 368, fig. 237) ; = *Ptychodera ceylonica*, Spengel, 1893, p. 359, and chart ; = *Ptychodera tricollaris*, Spengel, 1904*c*.

? *Ptychodera erythraea*, Spengel, 1893, p. 173, pl. x, figs. 1–20; 1904 *b*. Klunzinger, 1902. Gravier, 1905.

? *Ptychodera viridis*, Punnett, 1903, p. 656, pl. xxxvii, figs. 2, 6, 7 ; pl. xxxix, fig. 32 ; pl. xlii, figs. 17, 19.

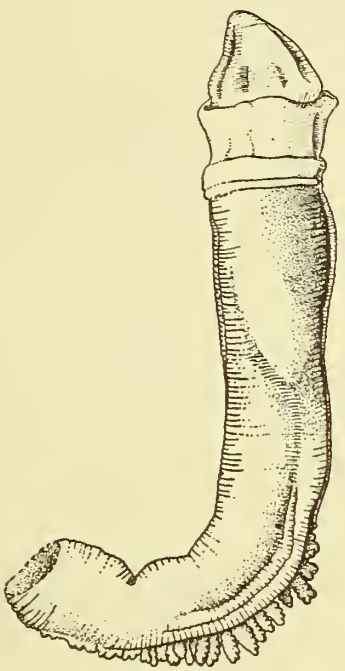
Eighteen specimens, of which nine, complete and apparently unregenerated, measure 27 to 50 mm. in total length ; from the Sand Flat, Low Isles, taken 20th April, 1929. Also three specimens 60 to 65 mm. long, from Low Isles, taken in August or September, 1928.

As the species is very variable it has been thought worth while to give some description of the Low Isles material. The three August–September specimens are much more slender than the others, and have smaller proboscis and collar ; although the branchial region is at least as long as in the others, the branchial basket is straight or only slightly sinuous in its course. They are evidently younger than the April animals—perhaps as much younger as the time between September, 1928, and April, 1929. Difference in method of preservation may further account for the difference in appearance. The following description applies to the April specimens only, but the measurements of the younger ones are included in the table.

* The type was incompletely described, and is not known to be now in existence.

† I am indebted for this reference to Spengel (1904*c*, p. 53). I have seen the second edition only.

External features (Text-fig. 1).—Proboscis usually conical, with fine transverse furrows and coarse longitudinal creases. Collar about equal in length to proboscis, with well-marked zones. " Racemose organ " well developed, simple and heart-shaped in young specimens, with three or four lobes in older. Length of collar 9 to $14\frac{1}{3}$ in total length, $\frac{3}{4}$ to $1\frac{1}{4}$ in length of branchial region. Origin of genital pleurae ventral in branchial region, rapidly becoming dorso-lateral behind it ; pleurae continued in hepatic region as a pair of ridges between dorsal and lateral saccules. Gill-openings long, narrow, curved slits ; branchial portion of pharynx an almost complete cylinder, communicating with the ventral portion by a narrow space between the parabranchial ridges, and exceeding it in girth. Branchial region separated from intestinal region by a short œsophageal tract to which the dorsal outline descends suddenly, rising as suddenly to about the same level



Text-fig. 1.—*Ptychodera flava.* Incomplete specimen measuring 33 mm., seen from the left side. The hepatic saccules are more numerous than appears, for in the region of the large caeca every alternate one is crowded towards the middle line and is invisible in side view.

behind it (*cf.* Text-fig. 2, A to D). External hepatic saccules visible 2 to $7\frac{1}{2}$ mm. behind pharynx, extending for 6 to 12 mm. ; saccules large, prominent, digitiform, mostly with well-developed anterior and posterior lobules ; six to ten anterior saccules dark in colour ; usually all but the smaller, anterior and posterior, saccules crowded into two ranks on each side.

The surface of the body is divided into annulations which are, as usual, somewhat irregular. These are much finer than in other specimens which I have examined (Willey's specimens from Isle of Pines ; types of most of the varieties from Maldives and Laccadives). In this respect and in general appearance and size the Low Isles material comes nearest to *Pt. flava* var. *maldivensis*, Punnett (1903, p. 648, pl. xxxix, fig. 27). The width of the annular ridges, and especially of the intervening furrows, is no doubt dependent upon the degree of contraction of the specimen, and this upon the muscular development of

the individual, which is probably influenced by its mode of life and must increase with age. The method of preservation must also be taken into account; the Low Isles April specimens were fixed in Bouin's fluid.

Measurements of Specimens of Ptychodera flava *from Low Isles.* (1–17, *April specimens;* 18–20, *August–September specimens.*)

	Total length.	Proboscis length. (mm.)	Length of collar. (mm.)	Width of collar. (mm.)	Length of branchial region. (mm.)	Branchial to hepatic region. (mm.)	Hepatic region.* (mm.)	Post-hepatic region. (mm.)	Collar-length (times in total length).	Collar-length (times in branchial length).	Notes.
1	50	4½	4	5	5	5	9	25	13	1·25	..
2	50	3½	3½	5	3	7	10	24	14·3	0·9	..
3	48	4	3½	5	4	6½	9	24	13·7	1·1	..
4	39	3	3	4½	2½	4	8½	17	13	0·8	..
5	34	3	3	4½	3	3	11	13	12·3	1	..
6	28	3½	2½	3½	2½	2	6½	13	11·2	1	..
7	27	2¾	3	4	2¼	2¾	6	13	9	0·75	..
8	21	3¾	2½	4½	2½	..	..	..	8·4	1	Anal region probably regenerated.
9	..	4	3½	5½	4	8	10	20	..	1·1	Incomplete.
10	..	4½	4	5½	6	7½	12	..	..	1·5	,,
11	..	4	3½	4½	2½	3½	9	..	..	0·7	,,
12	..	2½	3	4	3	3½	8	..	..	1	,,
13	..	4	3	4	2½	3	6½	..	..	0·8	,,
14	25	3½	3½	4½	5	5	1½	7½	..	1·4	Hepatic region and anus probably regenerated.
15	..	2½	2⅓	3½	2	2½	6	..	..	0·8	Incomplete.
16	..	4	3¼	4½	3	..	..	..	..	0·9	,,
17	47	2	2	3½	1	3½	10	30	..	..	Anterior end probably regenerated.
18	65	3	3	3½	4	6	10	39	21·6	1·3	..
19	60	3	3	3½	3	5	13	33	20	1	..
20	..	2	3	3⅓	6	6	7	..	..	2	Incomplete.

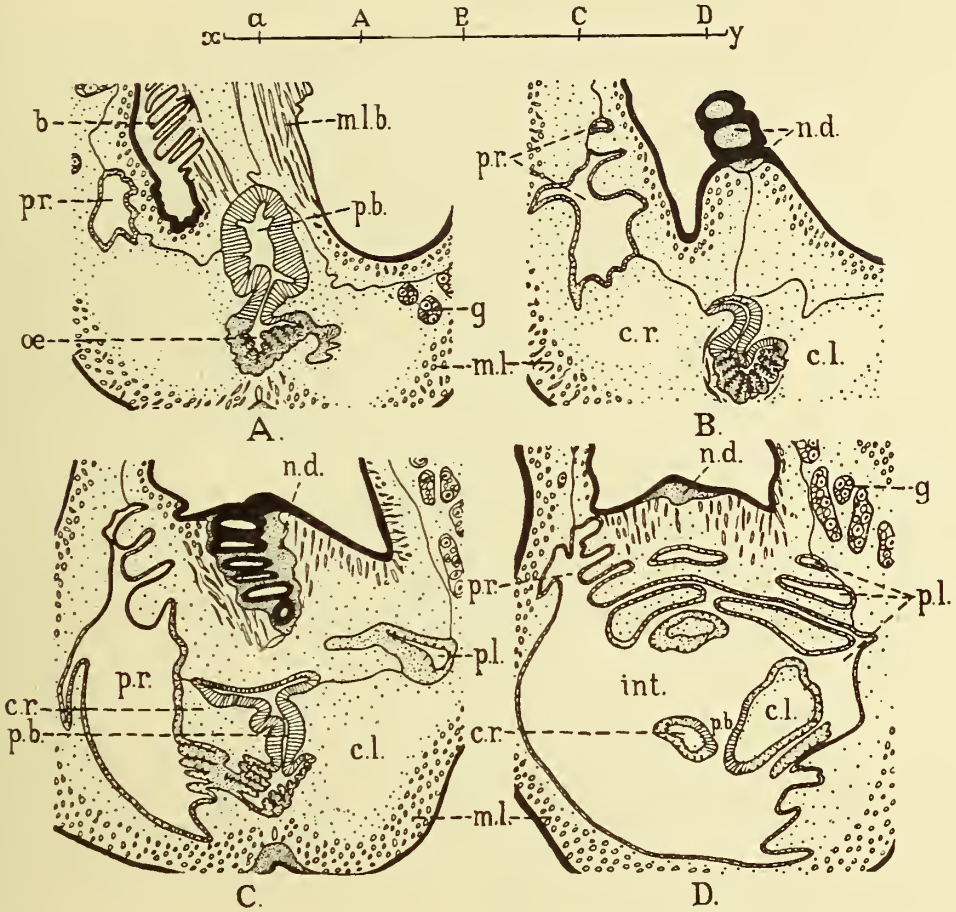
* External saccules.

Internal structure.—A single specimen, a male, 36 mm. long, was sectioned. Part of it was stained in picro-indigo-carmine and part in haematoxylin.

The *proboscis-musculature* is well developed, divided into groups by radial septa; circular connective-tissue fibres form a definite outline round the small anterior part of the proboscis-cavity. The left dorsal pouch of the proboscis-coelom is in open communication with the exterior by the *left proboscis-pore,* but the end-vesicle of the *right pore* does not communicate with the right dorsal pouch.

The *stomochord* gives off a pair of large lateral pouches without the mediation of a ventral caecum. The pouches have spacious cavities, which communicate by narrow channels near their posterior ends with the central cavity; the anterior end of the right pouch, still including a cavity, projects forward beyond the union of its wall with the central part of the organ. Anteriorly to this the ventral wall of the stomochord becomes thickened into an asymmetrical keel, into which the cavity presently descends, and which

forms the anterior end of the stomochord. In this specimen, therefore, in so far as a ventral outpushing of the stomochord can be spoken of, it is anterior to the lateral pouches, and the stomochord here attains a greater dorso-ventral thickness than between the pouches, where the depth is about one-fifth the length of the stomochord. This is the relative depth given by Spengel for *Pt. flava caledoniensis* (1903), p. 283, pl. xxiv, fig. 3), which he contrasts with *Pt. flava laysanica* (*loc. cit.*, pl. xxiv, fig. 4), where the ratio is $\frac{1}{6}$ to $\frac{1}{7}$. The shape of the organ in his two specimens is, however, entirely different, and is much



Text-fig. 2.—A, B, C, D. Transverse sections through the post-branchial region of *Ptychodera flava*, to show the relations of the lateral intestinal pouches (× 24). The line *x–y* represents 1 mm. (on a larger scale than the figures), and the points A, B, C, D along it the positions of the corresponding sections relative to each other and to *a*, the anterior end of the right pouch. *b*, dorsal ends of posterior branchial bars ; *c.l.*, coelom of left, and *c.r.* of right side ; *g.*, gonad ; *m.l.*, longitudinal muscles ; *m.l.b.*, dorsal longitudinal muscles of branchial region ; *n.d.*, dorsal nerve ; *oe.*, oesophagus ; *p.b.*, post-branchial canal ; *p.l.*, left intestinal pouch ; *p.r.*, right intestinal pouch. The thin nervous layer beneath the epidermis is omitted between dorsal and ventral nerves.

longer as well as slimmer in *Pt. flava laysanica* than in *Pt. flava caledoniensis*. All these differences are probably within the range of individual variation, which is very considerable in the allied *Pt. bahamensis* (Van der Horst, 1924, p. 51).

The *collar nerve-cord* has a continuous lumen, which is prolonged into the base of the single *dorsal root*. The distal part of the root is solid and is fused with the epidermis,

which is invaginated to meet it ; about halfway along the root is a transverse layer of yellowish pigment-granules. At the level of the root the nervous and epithelial layers of the floor of the neural cavity are thickened in the middle ; in front of this the floor is invaginated, making the nerve-cord kidney-shaped in section ; behind, it is roughly triangular. The perihaemal cavities contain much muscle, and embrace the ventral and lateral sides of the nerve-cord.

The " body " of the *skeleton* sends forward a pair of wings, which embrace the sides of the pouches of the stomochord. The " keel " is broad and excavated in front, narrow behind.

The *collar-pores* are typical in shape, and are associated with no thickening of the basement membrane such as is described in *Pt. bahamensis* (Van der Horst, 1924, p. 53.)

Sections of the branchial region are complicated by the sinuous course of the branchial basket. The ventral, non-perforated part of the pharynx is flattened, and its walls are thrown into folds, mainly as a result of contraction of the body-wall.

The *post-branchial region* differs somewhat from the description by Van der Horst (1930, p. 199) for specimens from Hawaii and New South Wales, and more resembles the usual condition for Ptychoderidae. It is probably as variable as most of the other internal characters which have been seized upon from time to time as specific. The parabranchial ridges consist of high cells with the nuclei near the periphery ; in the upper part of the ridge the bases of these cells are clear and remain unstained, but in the lower part they become abruptly pink (in haematoxylin), and glandular. At the posterior end of the branchial region, as the gill-slits become shorter the parabranchial ridges rapidly increase in height by the increase of the glandular area, and present broad flat surfaces to each other. After the last gill-slit they meet above to form the roof of the gut and are continued as the " post-branchial canal." It is perhaps more accurate to say that there is no " post-branchial canal," if this is to be considered as the posterior, unperforated part of the branchial basket. This dorsal part of the post-branchial gut is really an extension of the canal between the parabranchial ridges. The intestine sends forward a large right and a smaller left lateral pouch, and these fuse with the dorsal wall of high-celled part of the gut, and with the ventro-lateral wall of the low-celled oesophageal portion, so as to enclose finger-like coelomic pouches, which project backwards into the intestine. (These are stated to be absent in his material by Van der Horst, *loc. cit.*) These are illustrated in Text-fig. 2, D (*c.r.*, *c.l.*), where the last traces of the high mucous epithelium can be seen forming their mesial walls.

The *hepatic region* is typical.

The *pygochord* is a thin, flexible sheet of tissue, for which it is difficult to imagine a skeletal function. It is probably important in preventing eversion of the posterior end of the gut.

SPECIMENS OF *PTYCHODERA FLAVA* FROM THE GALAPAGOS ISLANDS.

Seven specimens of *Ptychodera flava* in the British Museum were collected by Dr. C. Crossland on the Pacific cruise of the yacht " St. George " (Scientific Expeditionary Research Association), 1923–24. They are from the Galapagos (Stations 3, 4 and 6), and thus increase the known range of the species. Two complete specimens, 57 and

58 mm. long, are included, and also a specimen of 20 mm., which shows, from the proportions of its anterior end, and the fact that the "racemose organ" has seven lobes, that it has regenerated the posterior end. They are more slender than the April specimens from Low Isles, and their annulations are farther apart. Their proportions are shown in the following table:

Total length.	Proboscis.	Collar.	Branchial region.	Pharynx to hepatic cæca.	Hepatic region.
57 mm.	$2\frac{3}{4}$ mm.	$1\frac{2}{3}$ mm.	$5\frac{1}{2}$ mm.	$7\frac{1}{2}$ mm.	13 mm.
58* ,,	$1\frac{2}{3}$,,	1 ,,	<1 ,,	6 ,,	15 ,,
65 mm. (incomplete)	3 ,,	$2\frac{1}{2}$–3 ,,	6 ,,	4 ,,	42 ,,
35 ,, ,,	3 ,,	$2\frac{1}{3}$,,	$4\frac{1}{2}$,,	4 ,,	21 ,,
34 ,, ,,	$2\frac{2}{3}$,,	$2\frac{1}{2}$,,	4 ,,	3 ,,	19 ,,
32 ,, ,,	$1\frac{3}{4}$,,	2 ,,	$5\frac{1}{2}$,,	5 ,,	10 ,,
20† ,, ,,	$3\frac{1}{2}$,,	3–$3\frac{1}{2}$,,	6 ,,	..	..

* Anterior end regenerated. † Posterior end regenerated.

REMARKS ON THE SPECIES OF *PTYCHODERA*.

Several species of *Ptychodera* have been described, some of them very fully; nevertheless the definition of species is a very difficult matter. Punnett (1903), working on the material from the Maldives and Laccadives, found that almost every little colony of *Pt. flava* had its peculiarities, and described no less than seven varieties, as well as two which he regarded as distinct species. Willey (1899) recognized a macrobranchiate and a microbranchiate form as extremes of a series, and found one form to predominate at one locality in New Caledonia, the other at another. Spengel (1903 and 1904) recognized a variety from Laysan, Sandwich Islands, another from Funafuti, both of which he considered distinct from the New Caledonia form. Recently Van der Horst, in material from Sydney and Hawaii, found specimens to agree with most of the previously described "varieties" of the species, and also a specimen (from Hawaii) which, although he regards it as belonging to *Pt. flava*, has all the characters of *Pt. erythraea*, Spengel, 1893, a very large Red Sea form. As far as the "varieties" are concerned, it seems best to follow Van der Horst and to regard *Pt. flava* as a very variable species, many of whose organs exhibit growth changes throughout life. It seems to attain a greater size in some localities than in others. Spengel, as well as Van der Horst, describes very large specimens from the Sandwich Islands, and *Pt. erythraea* from the Red Sea is probably, as Van der Horst suggests, also identical with *Pt. flava*. *Ptychodera viridis*, Punnett (1903, p. 656, pls. xxxvii, xxxix, XLII) was described from a few very small specimens, which, apart from juvenile characters, have nothing but their colour to separate them from *Pt. flava*.

Ptychodera asymmetrica, Punnett (*loc. cit.* p. 657, pl. xxxvii, figs. 1, *g*; pl. xlvi, figs. 52, 56, 58), described from eight specimens, in all of which the right genital pleura is devoid of gonads, may be distinct.

Ptychodera tricollaris (Schmarda), from Ceylon, is insufficiently described, and may be identical with *Pt. flava*.

Pt. pelsarti, Dakin (1916), from the Abrolhos Islands, off Western Australia, differs from *Pt. flava* in having the branchial basket smaller than the ventral part of the pharynx

with which it communicates by a wide channel between the parabranchial ridges. The suggestion that this is a juvenile character is supported by the association with it of weak musculature, a small and relatively simple " racemose organ " and a keeled skeleton. *Pt. flava* var. *saxicola*, Punnett (1903, p. 650, pl. xliv fig. 38) has a similar branchial region, and an incomplete specimen, including the posterior half of the pharynx, which I have examined, is as large or even larger than specimens of *Pt. flava* with long, curved gill-slits. It is possible that *Pt. flava* var. *saxicola* and *Pt. pelsarti* are identical, and distinct from *Pt. flava*.

Pt. bahamensis, Spengel, 1903, was originally described from a very young specimen, but Van der Horst (1924, pp. 50–55, pl. iv ; pl. vi, figs. 1, 9 ; pl. vii, figs. 7, 10, 12, 14) has described a large series of specimens of all sizes, up to more than 112 mm. in length, and these show growth changes similar to those of *Pt. flava*. It is difficult to see in what the two species differ. A small specimen in the British Museum, received from Dr. Van der Horst, does not differ externally from specimens of *Pt. flava* of a corresponding age. Van der Horst states (1924, p. 51) that the genital pleurae decrease in width behind the branchial region more gradually in *Pt. bahamensis* than in *Pt. flava* ; but there is much variation in *Pt. flava* in this respect, the extremes of which are illustrated in Willey's figures (1899, pl. xxvi, figs. 2, 3) of his macrobranchiate and microbranchiate forms. It is possible that short branchial region and rapid passage from broad to narrow pleurae may be expressions of a general stumpiness of form. The structure of the funnels of the collar-pores appears to be more complicated in *Pt. bahamensis* than in *Pt. flava*. Negative evidence in favour of the distinctness of *Pt. bahamensis* is found in the fact that, up to the present, identical Tornaria larvae of the type ascribed to *Ptychodera* have not been found in the Pacific and West Indian waters.

BALANOGLOSSUS CARNOSUS (WILLEY).

Ptychodera carnosa, Willey, 1899, p. 248, pl. xxvii, fig. 6 ; pl. xxviii, fig. 1*b* ; pl. xxix, figs. 16–19 ; pl. xxx, figs. 20–23.

Balanoglossus carnosus, Punnett, 1903, p. 640, pl. xxxvii, fig. 3. Maser, 1913. Van der Horst, 1930, p. 187, figs. 56–59.

The material from Low Islands consists of eight fragments, only one of which includes the anterior end. This has the following measurements :

Length of proboscis	10 mm.	
Length of collar	15 ,,	
Posterior diameter of collar	13 ,,	
Length of branchial region	40 ,,	(incomplete)
Width of each genital pleura, about . . .	5 ,,	

The base of the proboscis is narrower than its anterior part, and is surrounded by the anterior part of the collar, which leaves only 3 mm. free ventrally and about 7 mm. dorsally.

The collar consists of the usual three raised zones separated by two furrows ; the narrow posterior ridge is 1 mm. wide, the middle ridge 3 mm. ; the anterior region is constricted about midway in the total length of the collar in the manner characteristic of the species.

The gill-pouches have ventral caeca and open by small, oval or rectangular pores. The branchial portion of the pharynx is smaller in girth than the ventral part, from which it is separated by a narrow channel between prominent parabranchial ridges.

The remaining fragments are parts, 35 to 120 mm. long, about 9 mm. in diameter, of the posterior intestinal region of animals of about the same size as that represented by the anterior fragment. The largest, which includes the anus, contained a portion of another Enteropneust, a tubicolous polychaet in a tube of coarse sand 45 mm. long and about $3\frac{1}{2}$ mm. in diameter, a complete sand-anemone, a fly and some loose sand. The fact that most of these were in good condition suggests that the animal was making a hurried departure and swallowing every obstacle; it is possible that this heavily-laden posterior end was voluntarily discarded, as autotomy is known to occur in the species. The severed end of this fragment and of another were turned inside out and rolled back like a sleeve. Willey (1899, p. 256) states "an isolated piece, two or three inches long, of the abdominal region will always turn itself inside out," and, on the same page, "It breaks up into longer or shorter lengths upon slight provocation."

Dr. T. A. Stephenson tells me that "*Balanoglossus carnosus* was much more widespread" than *Ptychodera flava* "and was common on most sandy places; its presence could always be detected by its characteristic castings."

The species is recorded from Blanche Bay, New Britain (Willey), Minikoi and Hulule, Maldives (Punnett); Amboina and Kei Islands, E. Indies (Van der Horst), and Misaki, Japan (Van der Horst, and, *fide* Stiasny, 1928, Miyashita). This is the first record from the Australian coast.

The difficulty of recognizing good specific characters in adult Enteropneusta has been referred to in the case of *Ptychodera flava*. A similar problem surrounds *Balanoglossus carnosus*, which is one of a group of five described species, agreeing in the reduction of the proboscis, the enlargement of the collar (which supplements and largely replaces the proboscis as a burrowing organ), in the possession by the stomochord of dorso-lateral as well as ventral extensions, and by the gill-pouches of ventral caeca,* and in the abrupt ending of the genital pleurae. The other four species are *B. numeensis*, Maser, 1916, from New Caledonia, *B. biminiensis* and *B. jamaicensis* (Willey), 1899, from the West Indies, and *B. gigas*, Fr. Müller (Spengel, 1893), from Brazil. The resemblances of these five species to each other are much more remarkable than their differences, which reside in features shown by every fresh investigation to be subject to individual variation and growth changes. The differences between *B. carnosus* and *B. numeensis*, tabulated by Maser (*loc. cit.*, p. 422), are mainly dependent on the weaker development of the proboscis musculature, its skeleton and blood-supply in *B. numeensis*, the specimens of which were very much smaller than those of *B. carnosus*; it is possible that the shape of the collar and of the collar-pore are also connected with size. The length of the branchio-hepatic transition was compared in one specimen only of each species, and given as 10 mm. in *B. carnosus* (from Willey) and *nil* in *B. numeensis*. In Willey's figured specimen, now in the British Museum, it is only 2 mm. as preserved, so that individual variation is enough to account for the difference. *B. jamaicensis* was described by Willey from one poorly preserved, very large specimen, and Van der Horst (1930) considers it probably identical with *B. biminiensis*; this species resembles *B. carnosus* in all important characters, the chief differences being in size and correlated features. Of *B. gigas* less is known.

* *Balanoglossus clavigerus* also has gill-pouches with ventral cæca.

It is possible that we have to deal here with one circumtropical species. On the other hand, the evidence, admittedly incomplete, of the *Tornaria* larvae suggests that at any rate there are distinct West Indian and Indo-Pacific species. The solution, if there be one, of the problem may be arrived at by two methods of attack: (1) the examination of a large series of adults of different sizes from each locality, and (2) the working out of the life-histories. It is possible that the only absolute specific characters are larval, or even that the same species may produce slightly different larval forms in different localities.*

TORNARIA LARVAE.

Introduction.

The plankton samples include 79 specimens of Tornaria larvae, representing at least seven species. Of these, 71 specimens, of four species, are from the weekly plankton station, 3 miles east of Low Isles; the others were taken on one day at two stations outside Trinity Opening. With the exception of one specimen of the most abundant species, taken in April, all those from the weekly station were taken from the end of December, 1928, to February, 1929. Hauls were taken at Trinity Opening in August, September, October and November, but only the October hauls yielded Tornariae, and these were isolated specimens, of different species and ages, none of which appears to be identical with either of the species from nearer Low Isles. Speculations as to a restricted breeding season are hardly warrantable from these results.

The question arises as to which, if any, of the four species taken near Low Isles are the larvae of the two species in the collection of adults. The most abundant larva (*T. cairnsiensis*) may be that of *Balanoglossus carnosus* (but see below, p. 62). Stiasny-Wijnhoff and Stiasny (1926) conclude, on grounds of geographical distribution, that the larva of *Ptychodera* is a large, tentaculate Tornaria, with the coelom far from the gut and attached to the body-wall. The absence of a larva of this type from the collection is not enough to disprove this suggestion, but too little is known of the geographical distribution of the group to allow much weight to be attached to a theory based on such evidence alone.

In studying this collection full use has been made of the treatise on Tornaria larvae by Stiasny-Wijnhoff and Stiasny (1927)—a work indispensable to a student of the group.

Terminology.

As is well known, the Tornaria larva has, as well as a circular ring of cilia, two ciliated bands, a praeoral between the mouth and the apical organ, and a postoral, which loops round the body to meet the apical organ from the dorsal side. Between them is the oral field. In early stages these bands are relatively simple, but later they become thrown

* Calman (1909, p. 326) says of the Stomatopoda—"the larval forms of the various species differ from each other more widely than do the adults." *Rana temporaria* and *Rana arvalis* are so similar as adults as to have been long confused, but their tadpoles are easily distinguished (Boulenger, 1910, pp. 205–6). The same is true of *R. tigrina* and *R. cancrivora* (Boulenger, in Boulenger and Annandale, 1918, p. 65). Giard (1891 and 1892) gives several examples, from Coelenterata, Echinodermata, Crustacea, Insects and Tunicates, of animals of the same species which produce two or three forms of larvae according to environment or habits, and remarks that if one of these "poecilogonic varieties," as he terms them, should be accompanied by a difference, however small, in the adult, systematists would not hesitate to make it a distinct species (1892, p. 1551).

into a series of loops, between which the oral field forms a system of grooves, interdigitating with a corresponding system of ridges of the praeoral and postoral fields. The intricacy of the pattern so formed and the relative constancy of its main features necessitated the terminology introduced by Spengel (1893. pp. 371–73). Subsequent authors, including Stiasny-Wijnhoff and Stiasny, have followed Spengel in applying the term "Lobus" to branches of the groove-system of the oral field, whereas it is more descriptive of the intervening ridges and their outgrowths. For this reason, and also because some of the German words used cannot be literally rendered in English, I have not adopted this terminology as it stands. I have replaced the word "Lobus" by "groove," and translated "Sattel" as "ridge." Stiasny-Wijnhoff and Stiasny (*loc. cit.*, p. 49) reserve the term "Tentakel" for long, narrow, fringe-forming outgrowths of the edge between groove and ridge, while blunter processes, whether they turn outwards, as in *T. weldoni* and *T. setoensis*, or are flat, are called "sekundäre Sättel" and their possessors accordingly "nicht tentakulaten." In *T. setoensis* and similar larvae the outgrowths may project freely for half their length or more and may overlap each other; their attached basal parts alone have short secondary grooves between them. I propose for them the term "lobate tentacles." The word "lobate" is intended in a descriptive sense, but it fits equally well into the German terminology because of the association with "lobate tentacles" of short secondary grooves ("sekundäre Lobus"). Thus the secondary loops of the ciliated bands produce three types of structures, which grade into each other:

(i) Secondary ridges, with equal secondary grooves.
(ii) Lobate tentacles, with smaller secondary grooves.
(iii) Tentacles, with secondary grooves absent or very small.

Of these the last is the most specialized, as Stiasny-Wijnhoff and Stiasny point out.

A tabulated comparison of the German terminology and that adopted here follows. It is illustrated in Text-fig. 10 of this paper and the diagram of Stiasny-Wijnhoff and Stiasny (*loc. cit.*, p. 58).

	Stiasny-Wijnhoff and Stiasny (= Spengel, with additions).	In this paper.	
Oralfeld	Mundbucht	Oral arch	Oral field.
	Lateral lobus	Inferior lateral groove	
	..	Superior lateral groove	
	Primärer ventraler Lobus	Ventral groove	
	Obere primärer dorsaler Lobus	Superior dorsal groove	
	Unterer dorsallobus	Inferior dorsal groove	
	Sekundärer Lobus	Secondary groove	
Praeoralfeld	Mittelstreifen des Praeoralfeldes	Praeoral mid-ventral ridge	Praeoral field.
	Primärer Sattel (ventraler)	Ventro-lateral ridge	
Postoralfeld	Primärer Sattel (dorsaler)	Dorso-lateral ridge	Postoral field.
	Mittelstreifen des Postoralfeldes	Mid-dorsal ridge	
	Lateralsattel	Lateral ridge	
	Ventralband	Ventral belt	
	Ventralsattel	Postoral ventral ridge	
	Sekundärer Sattel	Secondary ridge or Lobate tentacle.	
	Tentakel	Tentacle.	

The names of larval stages are taken from Stiasny-Wijnhoff and Stiasny (1927).

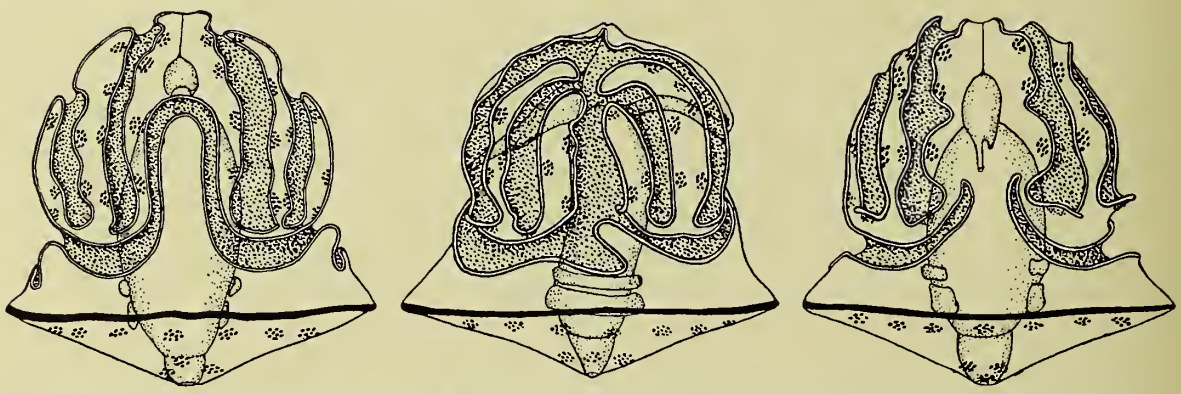
The number of tentacles or lobate tentacles appears to be a useful diagnostic character, and may be expressed in a formula. Thus, where V = ventral groove, L = superior lateral groove, D = superior dorsal groove, and the tentacles on the ventral border of each groove are enumerated before those on the dorsal border, the formula for *T. cairnsiensis* (Text-fig. 9) is V. 6–8, 6 ; L. 4, 4 ; D. 5 or 6, 5 or 6. Such a formula has the advantage over a diagram of showing the range of variation.

In naming new larval forms, the custom is followed of using " *Tornaria* " as though it were a generic name, and of deriving the specific name from that of one of its collectors, or of the locality where it was taken. A new name is given only when the Krohn-stage can be described and is clearly distinct from any other known Krohn-stage.

1. *Tornaria russelli*, sp. n. (Text-fig. 3).

Advanced Krohn-stage of a non-tentaculate larva.

Height $1\frac{1}{3}$ mm. ; diameter $1\frac{1}{3}$ mm.



TEXT-FIG. 3.—*Tornaria russelli.* Holotype. Ventral, right lateral and dorsal views (× 36). Oral field, in this and subsequent figures, indicated by dark shading.

Anterior part of larva bell-shaped, with greatest diameter at ciliated ring ; anal field a shallow inverted cone, the axis of which comprises $\frac{1}{5}$ of the total height. Praeoral field of a modified anchor-shape, with each lateral arm of the anchor forked to its base ; anterior part of postoral field similar.

Oral arch high, with parallel limbs ; upper and lower lips parallel. Inferior lateral groove triangular, with ventrally directed apex, bounded by a narrow, dorsally directed ridge on its ventral side and a scarcely perceptible eminence dorsally. Inferior dorsal groove long, with dorsal end turned upwards near middle line. Ventral, and superior dorsal grooves forked to correspond with the ridges. Praeoral and postoral ciliated bands with a wavy course, producing low secondary ridges and grooves ; on each side of mid-dorsal ridge a series of four secondary ridges, of which the lowest is largest and is separated from the next by a rather deep groove. Cushions of small (? pigment-) cells present on the ridges, principally on the secondary ridges, but not on the postoral ventral ridge or the ventral belt ; in addition, a ring of fifteen such cushions behind the ciliated ring and a group of nine round anus.

Proboscis-coelom ending in a right blind sac and a left dorsal pore. Paired collar- and trunk-coeloms close to gut, cylindrical, separate from each other. Oesophagus short, almost horizontal ; stomach cylindrical ; hind-gut small, conical,

A single specimen, from Station 19 (16° 20′ S., 146° 3′ E., outside Trinity Opening), taken 20th October, 1928, at 1 p.m., with the coarse silk tow-net (vertical haul, 180 metres of wire out).

I have associated with this species the name of F. S. Russell, Esq., D.S.C., D.F.C., B.A., who was in charge of the plankton investigations of the expedition.

This species is distinguished from all others by the deeply forked arms of the praeoral and postoral, anchor-shaped fields. It shows affinity to the group of Tornariae associated by Stiasny-Wijnhoff and Stiasny with the genus *Glandiceps*, and including *Tornaria menoni* Stiasny, from Madras (Ramunni Menon, 1903, p. 130, pl. x. figs. 5, 6 : also Stiasny-Wijnhoff and Stiasny, 1927, p. 118, figs. 44, 45), *T. dubia*, Spengel, from the Mediterranean (1893, p. 378, pl. xxii ; also Stiasny-Wijnhoff and Stiasny, 1927, p. 98, figs. 30–36), *T. mortenseni*, Stiasny, from Japan (1922, p. 124, figs. 1–5), and *T. ijimai*, Stiasny, from Japan (1928, p. 88, fig. 19 ; also below). *T. menoni* and *T. ijimai* have pigment-spots resembling the cushion-like groups of cells of *T. russelli* (which are colourless as preserved), but differing from them in details of distribution. The inferior lateral groove, which is invisible in a dorsal view of *T. russelli*, is situated so far ventrally in *T. menoni*, *T. dubia* and the type of *T. ijimai* that Stiasny has not identified it as a lateral groove. The forking of the ventro-lateral ridge is characteristic of the same three species, but the ridge and its divisions are very short, and there is no counterpart of the similar forked dorso-lateral ridge.

2. ? *Tornaria ijimai*, Stiasny (Text-fig. 4).

1928,* p. 88, fig. 19.

Below is a description of an opaque larva, probably of this species.
Height nearly 1 mm. ; diameter $\frac{4}{5}$ mm.

TEXT-FIG. 4.— *Tornaria ijimai*. Ventral, left lateral and dorsal views. (× 40.)

Shape a double cone. Ciliated ring much greater in diameter than any other part of larva ; axis of anal field about $\frac{2}{5}$ total height. Praeoral field divided by a pair of grooves of uncertain extent (somewhat damaged) into a mid-ventral and a pair of ventro-lateral ridges ; each ventro-lateral ridge subdivided by a narrow, shallow, secondary groove. Oral field narrow, consisting of a low oral arch, deep superior lateral grooves and long inferior dorsal grooves, approximating dorsally ; inferior lateral grooves small, triangular (preserved on one side only) ; superior dorsal groove represented by two indentations of the dorso-lateral margin of the postoral field. Ventral belt of postoral field broad,

* In this paper indebtedness is acknowledged to the manuscript of Miyashita. *T. ijimai* is described by Stiasny from Miyashita's reproductions of sketches made 15th July, 1895, by Prof. Ijima.

inclined at about 45° to plane of ciliated ring. A secondary circumanal ring about midway between this and anus.

Proboscis-pore to left of middle line ; shape of proboscis coelom not visible. Paired trunk-coelom present, apparently related to gut ; collar coelom ?.

A single specimen from Station 19 (16° 20′ S., 146° 3′ E., outside Trinity Opening), taken 20th October, 1928, at 1 p.m. in the 1 metre coarse silk net. (Vertical haul, 180 metres of wire out.)

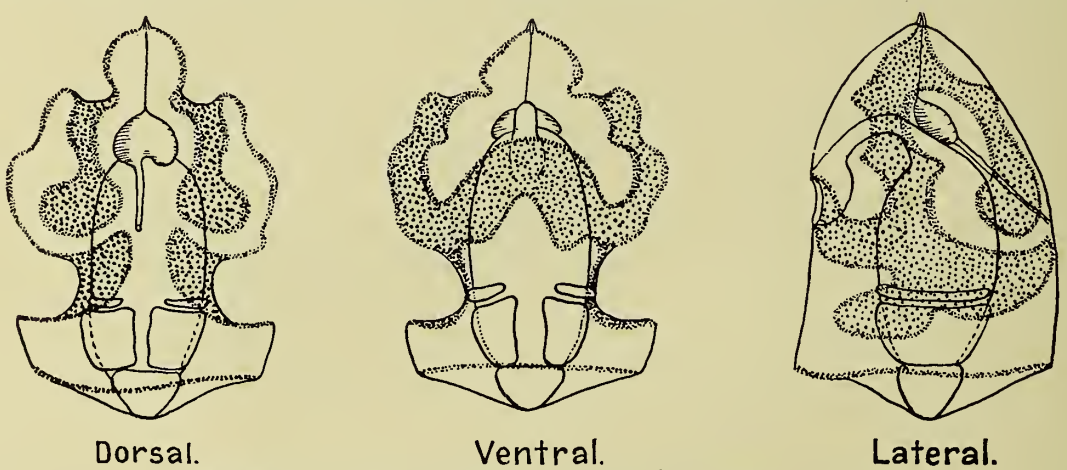
This specimen resembles *T. ijimai*, from Misaki, Japan, in the shape of prae- and post oral and anal fields, and in the low oral arch. Its opacity, the presence of a paired coelom, the narrowness of the grooves of the oral field and the greater diameter of the ciliated ring are differences indicating a more advanced stage of development. Other differences are the absence of pigment (as preserved), and the position of the inferior lateral groove ; this is more ventral in *T. ijimai*, as in *T. dubia* and *T. menoni*, and gives the postoral ventral ridge a peculiar triangular shape. The condition here described may have been arrived at by the reduction of the groove-system with age, but the specimen is not well enough preserved to allow stress to be laid on this character. This Tornaria is therefore considered to be identical with or closely related to *T. ijimai*, Stiasny.

3. *Tornaria colmani*, sp. n. (Text-figs. 5, 6).

Krohn-stage of a non-tentaculate larva.

Height about $\frac{5}{6}$ mm. ; diameter about $\frac{1}{2}$ mm.

Larva somewhat barrel-shaped, with shallow anal field, and with greatest diameter in region of longitudinal ciliated bands. Praeoral field five-lobed, the median lobe a little



TEXT-FIG. 5.—*Tornaria colmani.* Late Krohn stage. (× 60.)

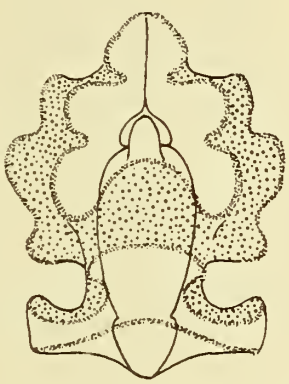
bigger than the lateral. Anterior part of postoral field anchor-shaped ; mid-dorsal ridge with a pair of broad, low secondary ridges ; dorso-lateral ridge with wavy outline, producing one secondary ridge on its dorsal border, two on its ventral. Oral field broad, oral arch low and wide. Postoral mid-ventral ridge triangular in older larva (Text-fig. 5), flat in younger (Text-fig. 6). Inferior lateral groove produced ventrally, bounded by a long, horizontal inferior lateral ridge on the ventral side, and a low prominence dorsally. Inferior dorsal groove broad and deep. Ventral belt of postoral field vertical or becoming narrower towards main ciliated ring. No secondary circumanal ring visible.

Proboscis-coelom a heart-shaped sac, the left lobe of which is connected by a narrow duct with the single left proboscis-pore, and the apex by a slender strand with the apical organ. No paired coelom in the younger larva; a large paired trunk-coelom and a narrow collar-coelom in the older larva, close to posterior part of stomach. Mouth wide, leading by a funnel-shaped cavity into the narrow oesophagus; stomach cylindrical, long, its end projecting into the conical hind-gut.

Two specimens, syntypes of the species, representing early and late Krohn-stages, from Station 40 (3 miles East of Low Isles, 6th February, 1929), taken at 3.50 p.m. in the fine silk tow-net.

The specific name refers to J. S. Colman, Esq., B.A., member of the Expedition, who worked on the animal plankton.

This larva evidently belongs to the "*Glandiceps*-type" of Stiasny-Wijnhoff and Stiasny. It resembles *T. dubia*, Spengel, in the shape and extent of the postoral field and inferior lateral groove, in the shallowness of the anal field and the absence from it of a secondary ciliated ring, but differs from it in the shape of the praeoral field, which is more



Text-fig. 6.—*Tornaria colmani*. Early Krohn stage. (× 60.)

like that of *T. ijimai*. The general resemblance to *T. mortenseni*, Stiasny (1922, p. 123, figs. 1–5), is striking, but the oldest stage of this described by Stiasny is a young Krohn-stage, and its height is given as $1\frac{1}{2}$ mm.; other differences are found in the shape of the stomach and of the inferior lateral groove, and in the presence in *T. mortenseni* of a secondary circumanal ring. The Barrier Reef larvae are therefore considered to represent a distinct species, related to *T. mortenseni*.

4. *Tornaria yongei*, sp. n. (Text-fig. 7).

A non-tentaculate larva in Krohn-stage.

Height = diameter = 1 mm.

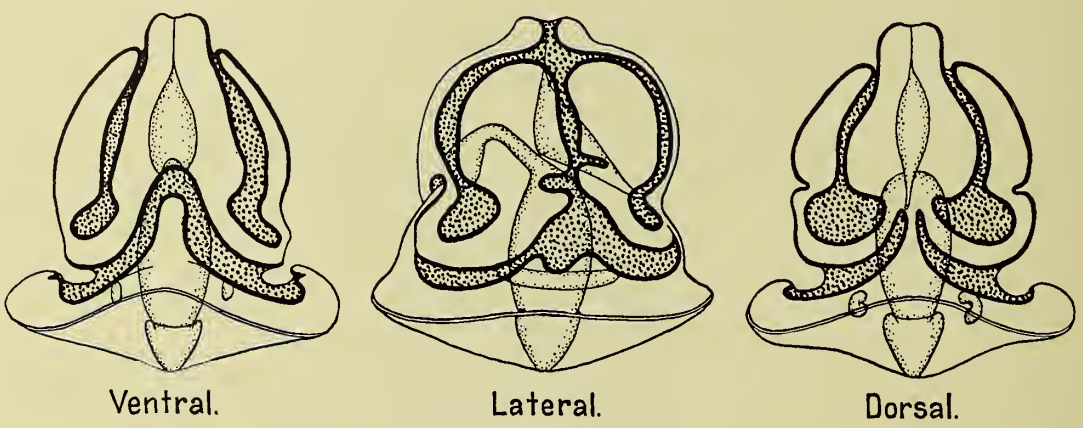
Anterior part of larva somewhat compressed laterally; greatest diameter at ciliated ring; postoral and anal fields meeting at a rounded edge, anal field a shallow cone. Praeoral and anterior part of postoral fields anchor-shaped. Oral arch rather low, narrow, oral field narrow, with shallow inferior lateral grooves, and long inferior dorsal grooves, nearly meeting mid-dorsally; superior lateral groove with a small secondary groove on each side, indenting the lower ends of ventro-lateral and dorso-lateral ridges; ventral groove and superior dorsal groove expanded at their lower ends. Apical organ situated

in a slight depression between the raised upper ends of praeoral and postoral fields. No secondary circumanal ring visible.

Proboscis-coelom fairly large, transparent, with a single, left dorsal pore. Paired trunk-coelom present, very transparent, cylindrical, curved; situated far from gut and almost equally far from body-wall. Mouth funnel-shaped; stomach small, cylindrical, projecting into the conical hind-gut.

A single specimen, from Station 40 (3 miles East of Low Isles, 6th February, 1929), taken at 3.50 p.m. in the fine silk tow-net.

I have associated with this species the name of C. M. Yonge, Esq., D.Sc., Ph.D., leader of the Expedition.



TEXT-FIG. 7.—*Tornaria yongei*. Holotype. (× 45.)

This larva belongs to Type I of Stiasny-Wijnhoff and Stiasny, and most closely resembles *T. bournei*, Stiasny (Bourne, 1889), which, with similar larvae, is considered by Stiasny-Wijnhoff and Stiasny (1927, pp. 83, 154, 157, 187) to belong to the genus *Glossobalanus*. *T. yongei* may possibly be the larva of *Gl. ruficollis* or *Gl. hedleyi*, both of which are known from this region.

5. *Young Non-tentaculate* Tornaria *Larvae.*

Five specimens, $\frac{2}{3}$ to $\frac{3}{4}$ mm. high, $\frac{1}{2}$ mm. in diameter, are too young to be assigned to any known species or to be described as new. They represent Metschnikoff- and early Krohn-stages of a Tornaria, probably of Type I of Stiasny-Wijnhoff and Stiasny. The following is a brief description of them.

Praeoral and anterior part of postoral fields anchor-shaped. Oral arch low, wide. Grooves of oral field fairly wide; inferior lateral groove shallow, bounded by simple inferior lateral ridges; inferior dorsal groove fairly long and broad; ventral, superior lateral and superior dorsal grooves each with two secondary grooves and ridges on each side. Ciliated band thickened on the secondary ridges. Apical organ in a slight depression between raised upper ends of praeoral and postoral fields. Mid-ventral postoral ridge of medium height and width. Anal field rather shallow; no secondary circumanal ring visible.

Proboscis-coelom weakly developed, narrow, transparent, with single, left pore. No trunk- or collar-coelom present. Stomach cylindrical or pear-shaped, projecting into the conical hind-gut.

Taken in the fine silk tow-net at Station 40 (3 miles East of Low Isles, 6th February, 1929, 3.50 p.m.).

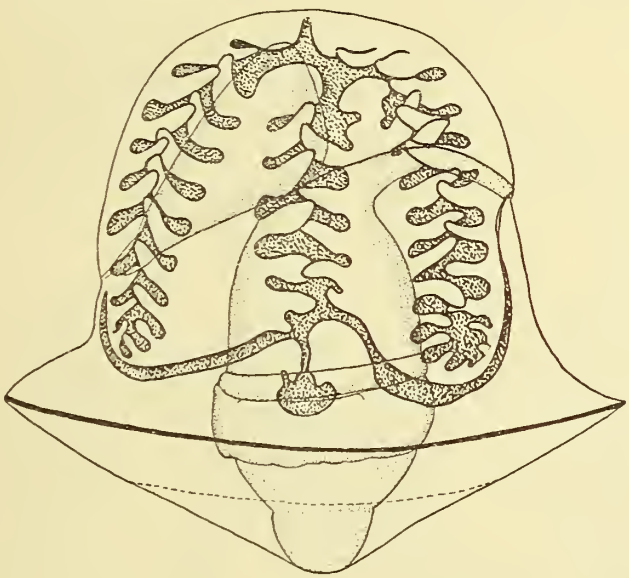
These are perhaps nearest to *T. yongei*, or may be an earlier stage of one of the larvae with lobate tentacles described below (pp. 55–62).

A Tornaria, $\frac{3}{4}$ mm. high, from Station 37, is very similar to these, but with the secondary ridges smaller, represented by the formula V. 2, 0 ; L. 2 or 3, 2 or 3 ; D. 0–1, 1. In the anal field is a broad ring of granular tissue like that forming the ciliated bands and their thickenings ; similar tissue surrounds the anus. This is reminiscent of the anal field of *T. russelli*, of which this may possibly be an early stage, before the forking of the primary dorso-lateral and ventro-lateral ridges has taken place.

6. *Tornaria setoensis*, Miyashita (Text-fig. 8).

Miyashita, 1925.* Stiasny, 1928, p. 73, figs. 5–7.

Below is description of an advanced Krohn-stage of a larva of this species : Height $2\frac{1}{2}$ mm. ; diameter $2\frac{3}{4}$ mm.



Text-fig. 8.—*Tornaria setoensis*. Lateral view. (× 30.)

Upper part of body bell-shaped, with flat apical region ; anal field an inverted cone with axis less than $\frac{1}{3}$ total height. Grooves deep, with overhanging edges, narrower than the ridges. Praeoral field anchor-shaped.

Oral arch narrow, high. Inferior lateral grooves flask-shaped, with a pair of outturned processes on the inferior lateral ridges. Inferior dorsal grooves narrow, turned upwards near mid-dorsal line, where they leave a narrow isthmus. Tentacles lobate, overlapping, free for more than half their length, the upper with ends turned upwards, not extending round upper ends of ridges ; tentacle formula, V. 11 or 12, 9 or 10 ; L. 5 or 6, 5 or 6 ; D. 8 or 9, 9 or 10. Mid-dorsal and praeoral mid-ventral ridges presenting parallel edges near apex, at which they are continuous ; apex not invaginated ; no eyespots discerned. Ventral belt nearly horizontal. Main ciliated ring irregularly wavy (simplified in figure). Secondary circumanal ring probably present, but invisible for most of its length.

* For the reference to this paper, which I have not seen, I am indebted to Stiasny's paper (*loc. cit.*).

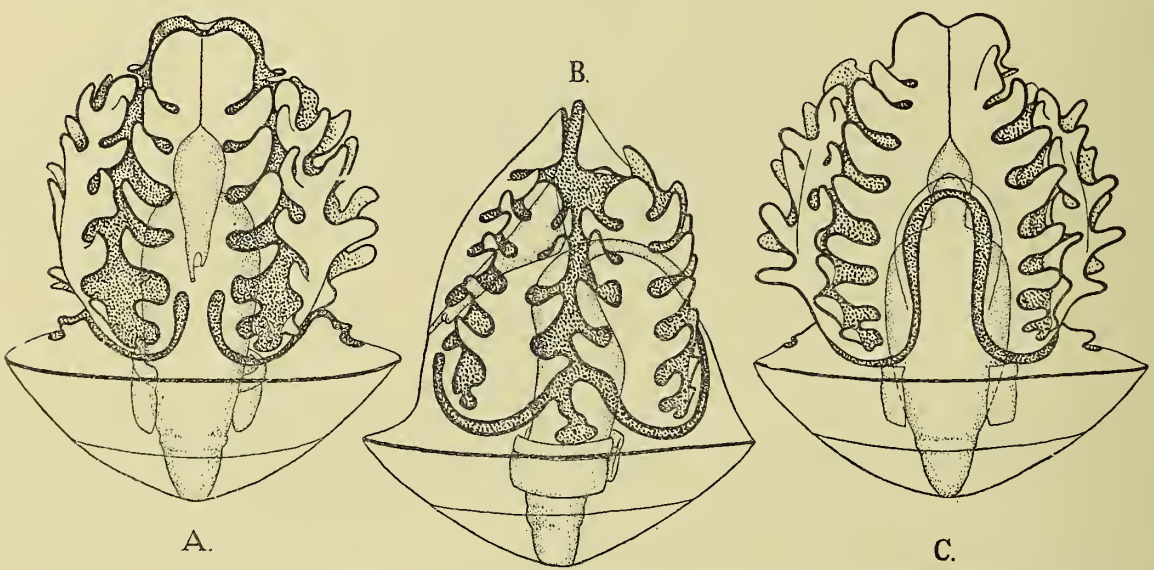
Proboscis-coelom large, with a single, left pore. Paired trunk- and collar-coeloms present, distinct but adjacent, transparent, close to gut, somewhat rounded, but not cylindrical.

A single specimen, from Station 19 (16° 20′ S., 146° 3′ E., outside Trinity Opening), taken 20th October, 1928, at 1 p.m., with the 1 metre coarse silk tow-net (vertical haul, 180 metres of wire out).

This Tornaria is considered to be specifically identical with *T. setoensis*, with which it shows a striking agreement in number of lobate tentacles,* shape of inferior lateral grooves and ridges and of the postoral ventral ridge, flatness of apical pole, etc. Certain differences suggest that this is a more advanced stage than that figured by Stiasny ; the body-wall is semi-opaque ; the proboscis- and collar-coeloms are larger ; the diameter of the ciliated ring is relatively greater ; the lobate tentacles are rather flabby, and meet or even overlap across the grooves. The slightly smaller size of the Barrier Reef specimen may be due to the shrinkage characteristic of the regressive phase of larval development.

7. *Tornaria cairnsiensis*, sp. n. (Text-figs. 9–11).

A larva with lobate tentacles.
Krohn-stage (Text-fig. 9).
Maximum height 2 mm.



Text-fig. 9.—*Tornaria cairnsiensis*. Holotype. Dorsal, right lateral and ventral views. (× 30.)

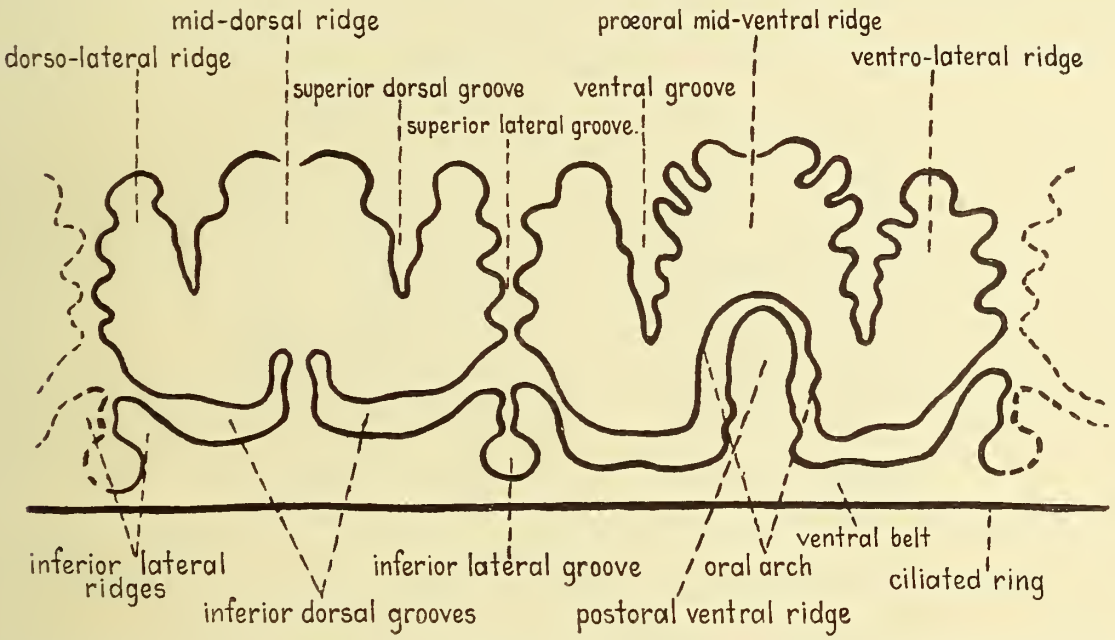
Shape a double cone ; height greater than diameter of ciliated ring ; axis of anal field about $\frac{1}{3}$ total height in later Krohn-stage, less in younger larvae. Praeoral field anchor-shaped.

Grooves of oral field about as wide as the ridges. Oral arch rather high and narrow. Inferior lateral grooves flask-shaped, bounded by large inferior lateral ridges, of which

* It is difficult to understand why Stiasny, in his diagram (*loc. cit.*, p. 74, fig. 7), shows the tentacles continued round the tops of the ridges, whereas his drawings show the ridges ending, as here, in a lobe as big as two tentacles, or why the number of tentacles bordering the superior lateral groove is greater in his diagram than in his drawings.

the ventral is usually larger ; a pair of blunt processes at neck of flask. Inferior dorsal grooves long, narrow, curved upwards dorsally, with a narrow isthmus between them. Tentacles lobate, with ends turned upwards and overlapping, not continued round upper ends of ridges ; V. 6–8, 6 ; L. 4, 4 ; D. 5 or 6, 5 or 6. Mid-dorsal ridge ending above in a broad lobe, which meets a similar, larger, ventral lobe, the two being reared up against each other so that the apical organ is slightly invaginated. Apical organ with a pair of eye-spots. Ventral belt of postoral field inclined at a small angle to the horizontal plane ; greatest diameter of larva at ciliated ring. A secondary, transparent, circumanal ring, usually visible, mid-way between this and anus.

Proboscis-coelom with a single, left pore. Paired trunk- and collar-coeloms present, close to stomach ; collar-coelom narrow, attached to anterior border of trunk-coelom. Oesophagus slightly curved ; stomach ovoid ; with narrow end projecting into hind-gut.



Text-fig. 10.—*Tornaria cairnsiensis*. Projection of course of ciliated bands in a specimen $\frac{3}{4}$ mm. high. Secondary circumanal ring omitted.

Described from twelve specimens, $1\frac{1}{2}$ to 2 mm. high, from Stations 37 and 39, 3 miles East of Low Isles, 14th and 30th January (one in the fine, three in the coarse silk net, and two in the stramin net, St. 37 ; the rest in the stramin net, St. 39). These are at the height of larval development and are well preserved and transparent, forming some of the most beautiful objects of the plankton.

In addition, earlier stages are represented by :

(*a*) A single specimen (Text-fig. 11), $\frac{7}{8} \times \frac{3}{4}$ mm., taken in the coarse silk net at Station 38 (21st January, same locality).

(*b*) Four specimens, $1\frac{1}{4}$ to $1\frac{3}{8}$ mm. high, from the stramin net at Station 39.

(*c*) Thirty-eight specimens, $\frac{3}{4}$ to $1\frac{1}{2}$ mm. high, taken in the coarse silk net at Station 39.

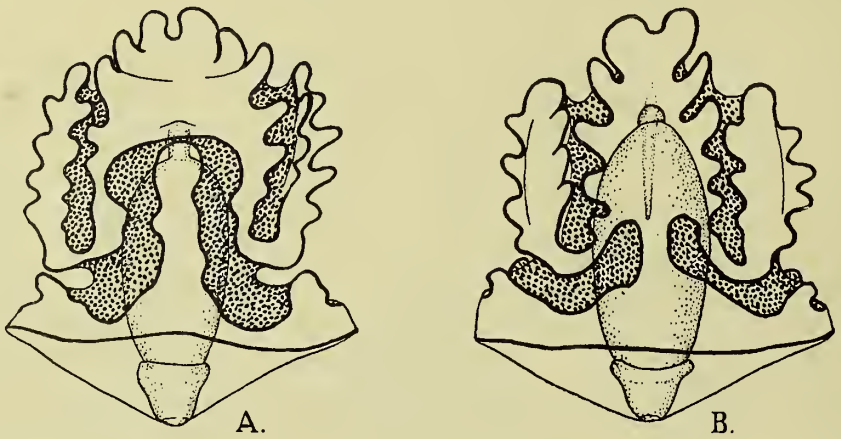
(*d*) A single specimen, 1 mm. high, taken in the coarse silk net at Station 52 (6th April, 1929, same locality).

One specimen, $1\frac{1}{4}$ mm. high, from Station 37, and two, about 1 mm. high, from Station 39, taken in the coarse silk net appear to be in an early regressive stage.

From this material five stages may be described.

(i) Height $\frac{3}{4}$ mm., diameter less than height. Transparent. First-formed parts of oral field wide ; ventral and superior dorsal grooves short ; " tentacles " short, few, in process of formation, those of superior lateral groove in advance of the others. Presence of secondary circumanal ring doubtful. Proboscis-coelom slender, transparent ; no paired coelom. Represented by a single specimen from St. 39 (Text-fig. 10).

(ii) Height less than 1 mm. ; diameter less than height. Transparent. Grooves of oral field wide ; ventral and superior dorsal grooves fully formed ; " tentacles " short, four on each side of superior lateral groove, those on ventral and superior dorsal grooves few, in process of development. Secondary circumanal ring present or absent. Proboscis-coelom a narrow, transparent tube, with pore. No paired coelomic sacs. Represented by the specimen from St. 38 (Text-fig. 11), and a few, less well preserved, from St. 39.



Text-fig. 11.—*Tornaria cairnsiensis*. Ventral and dorsal views of a specimen $\frac{7}{8}$ mm. high. (×60.)

(iii) Height 1 to $1\frac{1}{2}$ mm. ; diameter less than height. Transparent. Grooves of oral field narrow ; tentacle-formula V. 5–6, 4–5 ; L. 4, 4 ; D. 3–5, 5 ; inferior lateral ridge with rudiment of tentacle-like process. Secondary circumanal ring usually visible. Proboscis-coelom rounded, transparent ; paired trunk-coelom and usually also collar-coelom present, small, transparent, wafer-like. Anal field conical. Several specimens from St. 37, 39 and 52.

(iv) Height $1\frac{1}{2}$ to 2 mm. ; diameter less than height. Transparent. Tentacles well formed, firm ; V. 6–8, 6 ; L. 4, 4 ; D. 5 or 6, 5 or 6 ; inferior lateral ridge with tentacle-like process. Secondary circumanal ring usually visible. Proboscis-coelom somewhat opaque and muscular ; trunk and collar coeloms transparent, larger than in previous stage, but still flattened in a plane parallel to gut-wall. Anal field with sides more convex, almost a sector of a sphere ; wall of anal field with tendency to be more opaque than rest of body-wall. Larval development at its climax. Represented by the eleven specimens described (Text-fig. 9).

(v) Height from a little less than 1 mm. to $1\frac{1}{4}$ mm. : diameter nearly or quite equal to height. Semi-opaque. Anterior, tentacle-bearing part of larva shrunken, somewhat depressed (but apical organ still invaginated between adpressed upper ends of praeoral and postoral fields) : tentacles with tendency to become flabby ; tentacle formula as stage (iv), but in one specimen apparently only three on either side of superior lateral groove. Inferior lateral ridge with out-turned process. Secondary circumanal ring visible in one specimen. Anal field shaped like a flat-rimmed bowl. Proboscis-coelom opaque ; trunk- and collar-coeloms adjacent, curved cylinders, with semi-opaque walls. Early regressive (" Krohn-Spengel ") stage. Represented by three specimens, none of which is sufficiently perfect or well preserved to be figured, from Stations 37 and 39 (coarse silk net).

The first two of these stages correspond most nearly to the Metschnikoff-stage of Stiasny-Wijnhoff and Stiasny, but differ from it in the presence of secondary ridges or lobate tentacles. The third and fourth are early and late Krohn-stages, but differ from the typical Krohn-stage in the early development of the collar-coelom. The fifth stage differs from a typical Spengel-stage in the retention of the lobate tentacles and relative transparency of the body-wall.

The youngest stage described here is very similar to *T. wynhoffi*, Stiasny (1928, p. 76, figs. 8 and 9), from Seto, near Osaka, Japan. The chief differences are the broader oral field and horizontal upper lip of *T. wynhoffi* ; these may simply indicate an earlier stage of development, and it is possible that the two species are identical. Another possibility is that *T. wynhoffi* is a young *T. setoensis*, which must be very similar to *T. cairnsiensis* in the earlier stages. The size of *T. wynhoffi* was unknown to Stiasny.

T. cairnsiensis differs from *T. setoensis* in the shape of the apical region and number of lobate tentacles. The constant presence of four of these on either side of the superior lateral groove in specimens of 1 to 2 mm. is very striking, and it is unlikely that *T. cairnsiensis* ever attains the size of known specimens of *T. setoensis*.

Two other Tornarias which come up for comparison are *T. ritteri*, Spengel, from the Californian coast (Ritter, 1894 : Ritter and Davis, 1904), and *T. weldoni*, Stiasny, from the Bahamas (Stiasny, 1921*a* ; the specimen described by Morgan in 1894 does not compare so closely). These both have lobate tentacles and a convex anal field, with secondary circumanal ring. The numbers of tentacles correspond very closely, but *T. ritteri* appears to have fewer (" about three ") on each side of the superior lateral groove. In the diagram of *T. weldoni* (Stiasny, 1921*a*, p. 4, fig. 1) there are four or five tentacles in this position, but the figures (pl. i, figs. 2–5) show only two or three, less well-formed than those of the dorsal groove.

T. ritteri differs from *T. cairnsiensis* in the following characters :

(i) Oral arch wider and lower.
(ii) Ventral belt apparently wider and steeper.
(iii) Dorso- and ventro-lateral ridges shorter.
(iv) Lobate tentacles shorter, not meeting across grooves.

T. weldoni differs from *T. cairnsiensis* in the following characters :

(i) Excess of diameter over height.
(ii) Absence of tentacle-like processes on inferior lateral grooves.
(iii) Collar-coelom separate from trunk-coelom.

8. *Tornaria* sp., near *T. cairnsiensis* (Text-fig. 12).

Krohn-Spengel stage of a larva with lobate tentacles.

Height 1 mm. ; diameter $1\frac{1}{6}$ mm.

Upper part of body dome-shaped, with flat apical pole ; axis of anal field about $\frac{1}{4}$ total height. Body-wall somewhat opaque. Oral arch high, narrow. Grooves of oral field narrow. Inferior lateral grooves flask-shaped, with prominent inferior lateral ridges, each with a blunt, tentacle-like process at neck of flask. Tentacles of a rather slender lobate type, projecting outwards ; two tentacles and the rudiment of a third (indicated by " $\frac{1}{2}$ " in the formula) on superior lateral groove ; tentacle formula V. 8, 6 ; L. $2\frac{1}{2}$, $2\frac{1}{2}$; D. 5, 6. Structure of apical organ not visible. No secondary ciliated ring detected.

TEXT-FIG. 12.—*Tornaria* sp. from Station 19. Right lateral view. (×45.)

Two pairs of cylindrical coelomic sacs close to gut, the collar-coelom adjacent to the trunk-coelom.

A single specimen from Station 19, taken in the same net as *T. setoensis*.

This Tornaria differs from the early regressive stage of *T. cairnsiensis* in the flatness of the apical pole, shallower anal field, and the presence of only two or three tentacles on either side of the superior lateral groove, although these are firm, and show no signs of degeneration. The poorness of the material of the corresponding stage of *T. cairnsiensis* makes a decision as to the specific distinctness of this specimen impossible at present.

It resembles *T. setoensis* in shape, as well as in time and place of capture, but the two are at almost the same developmental stage, and the difference in size and in number of tentacles seems too great for specific identity.

9. *Tornaria* sp. from Station 20 (Text-fig. 13).

Late Krohn-stage of a larva with lobate tentacles.

Height $1\frac{1}{4}$ mm.

Shape a double cone. Diameter nearly equal to height ; anal field convex, with axis a little less than $\frac{1}{3}$ total height. Body-wall translucent.

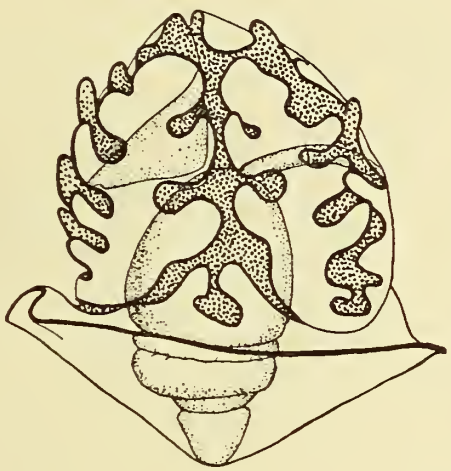
Inferior lateral ridges almost rectangular, without tentacle-like processes ; inferior lateral groove roughly flask-shaped. Well-developed inferior dorsal grooves. Praeoral field anchor-shaped. Tentacles lobate, rather short ; V. 6, 4 ; L. 2 or $2\frac{1}{2}$, 2 ; D. 4, 4,

Apical organ slightly invaginated ; upper ends of prae- and postoral fields meeting at an obtuse angle. No secondary circumanal ring.

Proboscis-coelom with a single, left pore. Paried trunk-coelom present, close to gut, with adjacent collar-coelom.

A single specimen from Station 20 (16° 19′ S., 146° 7′ E., outside Trinity Opening), taken 20th October, 1928, at 11.35 a.m., in the Nansen vertical net, with 250 metres of wire out.

This Tornaria differs from specimens of *T. cairnsiensis* of the same size in the apparent absence of a secondary circumanal ring, and in having only two tentacles, or two and a small rudiment, on either side of the superior lateral groove.



Text-fig. 13.—*Tornaria* sp. from Station 20. Right lateral view. (× 45.)

It differs from the small Tornaria with lobate tentacles from Station 19 (Text-fig. 12) in general shape and in having shorter, thicker tentacles, fewer on the dorsal and ventral grooves, and simpler inferior lateral ridges. It is perhaps nearest to *T. weldoni*, Stiasny, 1921*a*, in which the chief difference is the presence of a secondary circumanal ring at a corresponding stage.

10. *Regressive Stage* (*Spengel Stage*) *of a Larva with Lobate Tentacles* (Text-fig. 14).

Height $1\frac{1}{2}$ mm. ; diameter $1\frac{3}{4}$ mm.

Diameter of ciliated ring much greater than that of any other part. Upper part of larva swollen, depressed, with flattened, invaginated apical pole. Anal field shaped like a flat-rimmed bowl, its axis comprising $\frac{2}{5}$ total height of larva.

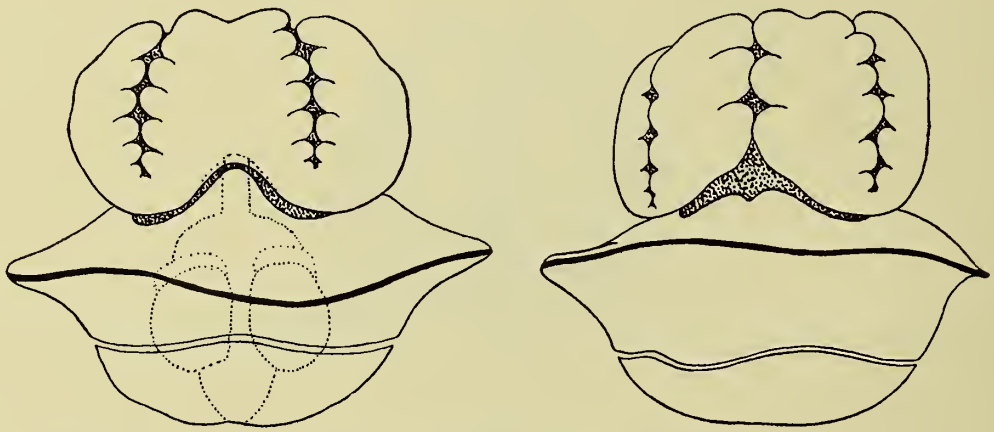
Body-wall opaque. Grooves of oral field narrow, overhung by the swollen ridges ; no praeoral and postoral ciliated bands visible. Praeoral field of anchor-shaped type. Oral arch low, enclosing a wide angle. Inferior lateral groove almost imperceptible, bounded by low eminences. Inferior dorsal groove long and deep. Tentacles represented by blunt, rounded secondary ridges, separated by narrow secondary grooves ; tentacle formula V. 6 or 7, 5 or 6 ; L. 2, 2 ; D. 4 or 5, 6. Anal field with secondary circumanal ring midway between anus and main ciliated ring.

Proboscis-coelom with a single left pore. Paired trunk-coelom close to gut, with narrow collar-coelom attached to it in front.

A single specimen from Station 19 (16° 20′ S., 146° 3′ E.), taken 20th October, 1928, at 11.42 a.m., in the Nansen vertical net (180 metres of wire out).

The body-wall is broken along the line of the secondary, circumanal ring, and only through this break could the internal organization be made out.

In number and proportions of the secondary ridges (or lobate tentacles) this most resembles the Tornaria from Station 20 (Text-fig. 13), which, however, appears to lack a secondary circumanal ring. If, as seems probable, it is a later stage of this, or some other larva with lobate tentacles, it is interesting to note that ridges, representing the "tentacles,"



TEXT-FIG. 14.— *Tornaria* in regressive stage. Ventral and lateral views. (× 40.)

persist when there is no longer any trace of praeoral and postoral ciliated bands, at least in surface view. In the very similar *Tornaria weldoni*, Stiasny, however, it appears that the ridges vanish by the simplification of the still visible ciliated band (*cf.* Stiasny, 1921*a*, pl. i, fig. 5).

Association of Larvae with Lobate Tentacles with Adults.

Larvae with lobate tentacles are considered by Stiasny to belong to *Balanoglossus* or *Glossobalanus*, since they are not very different from the Tornaria of *B. clavigerus*, the only Enteropneust with indirect development whose life-history has been worked out. *T. weldoni* was found where *B. biminiensis* is the common Enteropneust, and it is probable that one of the species here described belongs to the closely related *B. carnosus*. *B. carnosus* is a giant species, and this fact suggests that the largest Tornaria in question, *T. setoensis*, may belong to it. This suggestion has already been made by Stiasny (1928), in view of the association of the two in Japanese waters. Another possibility is that *T. cairnsiensis* may belong to *B. carnosus*, (see above p. 48). Speculations as to the identity of these Tornarias are, however, of little use until more is known of the Enteropneust fauna of the region, and it is very desirable that more life-histories should be worked out.

11. ? *T. delsmanni*, Stiasny-Wijnhoff and Stiasny.

"Die Tornaria von Madoera" (*T. delsmanni*), Stiasny-Wijnhoff and Stiasny, 1927, p. 163, figs. 78, 79.

Three stages are represented in this collection, each by a single specimen:

(i) Metschnikoff-Krohn stage (Text-fig. 15). Height $1\frac{1}{4}$ mm.; diameter 1 mm.

Bell-shaped, with almost flat anal field: diameter of ciliated ring but little greater than that of anterior part of larva. Grooves of oral field broad and shallow. Praeoral field and anterior part of postoral field with very narrow bridges between their median and lateral portions.

Oral arch rather broad. Postoral mid-ventral ridge high, narrow. Inferior lateral grooves present, bounded by simple ridges, that on the ventral side the larger. Inferior

Text-fig. 15.— ? *Tornaria delsmanni*. Metschnikoff-Krohn stage (× 40.) The inner surfaces of the tentacles, although strictly part of the oral field, are left white here and in Text-figs. 16 and 17.

dorsal groove broad, not expanded dorsally. Tentacles narrow, rather short, the lower rudimentary; V. 8 or 9, 7 or 8; L. 7 or 8, 7 or 8; D. 7, 7 or 8. Ciliated bands ending at apical organ, which is but little invaginated. Ventral belt of postoral field narrow, almost vertical. A secondary, transparent, circumanal ring close to main ciliated ring.

Proboscis-coelom a narrow strand of tissue, with a single pore near mid-dorsal line. No paired coelom. Oesophagus short, almost horizontal; stomach cylindrical, projecting into a small, conical hind-gut.

A single specimen, from Station 38 (3 miles East of Low Isles, 21st January, 1929), taken at 10.20 a.m. in the coarse silk net.

(ii) Krohn-stage (Text-fig. 16). Height nearly 3 mm.; diameter $2\frac{3}{4}$ mm.

Shape a double cone; anal field rather shallow, its axis about $\frac{1}{6}$ total height. Praeoral field and anterior part of postoral field anchor-shaped.

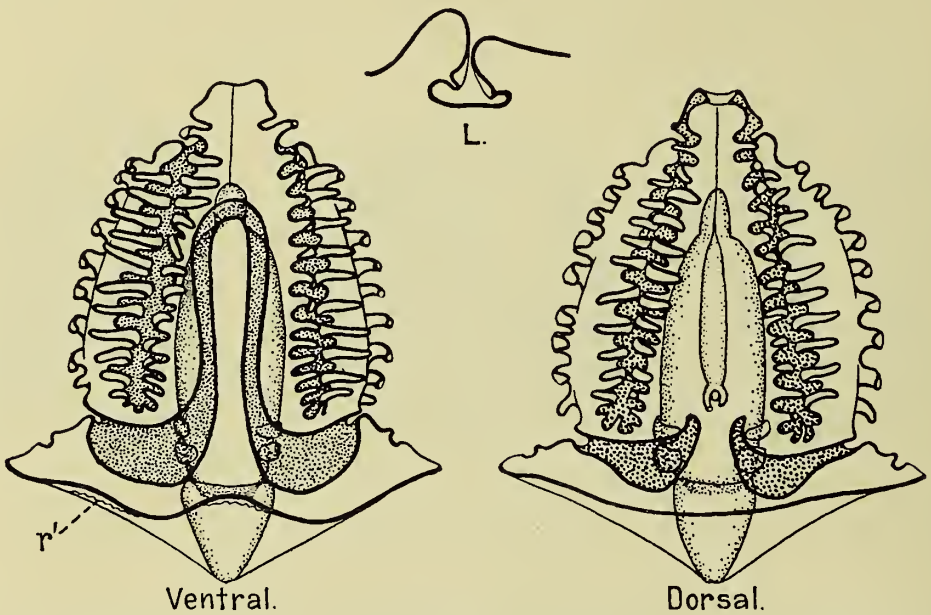
Oral arch and postoral mid-ventral ridge high, narrow. Inferior lateral grooves flask-shaped, with a short, tentacle-like process on each of the inferior lateral ridges, of which the ventral is higher than the dorsal. Inferior dorsal groove deep, somewhat expanded dorsally. Tentacles long, narrow, turned outwards and usually reflexed over ridges, continuous round lower ends of grooves, but not round upper ends of ridges. Tentacle at base of each dorsal groove longer than those next to it; V. 13–15, 10 or 11;

L. 9, 9 ; D. 11, 12–14. Ciliated bands ending at apical organ ; upper ends of praeoral and postoral fields meeting at an acute angle, so that apex is visible from dorsal side only. A secondary circumanal ring close to main ciliated ring.

Proboscis-coelom narrow, with two short ducts, only the left of which opens by a pore. Stomach cylindrical, not wider than hind-gut, which is unusually long. Paired trunk- and collar-coeloms present, close to gut, separate from each other.

A single specimen, from Station 37 (3 miles East of Low Isles, 14th January, 1929), taken at 9.40 a.m. in the fine silk tow-net.

(iii) Spengel stage (Text-fig. 17). A fragment, consisting of the left postero-dorsal portion of the larva. This differs from the complete specimen in the greater development



Text-fig. 16.—? *Tornaria delsmanni*. Krohn stage. (× *ca.* 22.) *L.*, inferior lateral ridges, more highly magnified ; *r'*., secondary, circumanal ring.

of the paired coelomic sacs, the broad, rather opaque proboscis-coelom, and the apparent absence of a secondary circumanal ring. The radius of the shallow anal field is about 1 mm. ; the diameter was therefore probably not greater than that of the Krohn-stage. Eleven tentacles are present on one side of the most nearly complete dorsal groove. At the lower end of the superior lateral groove is an oval, cushion-like thickening of the epidermis, with a groove along its longer, dorso-ventral axis (Text-fig. 17, *ep. o.*). This is in the wrong position for a collar-pore or gill-pore, and in any case is quite unconnected with oesophagus or collar-coelom. The tissue around it is well preserved and it has the appearance of a normal structure.

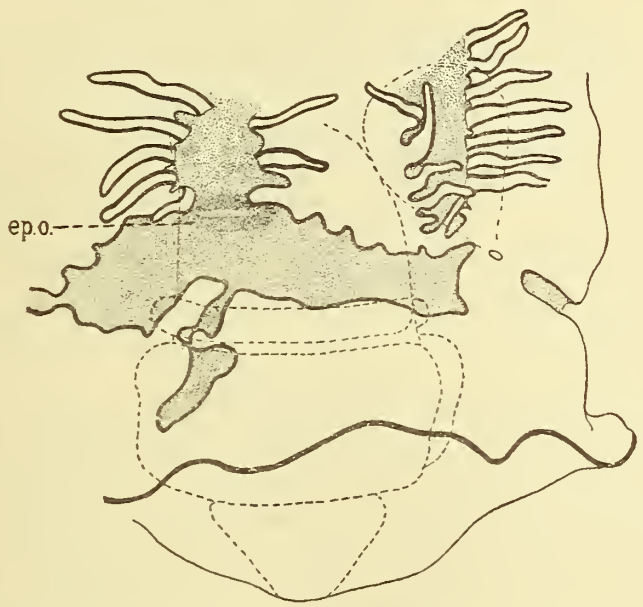
Taken at Station 35 (3 miles East of Low Isles, 27th December, 1928), at 10.18 a.m. in the stramin net.

This fragment is probably of the same species as the other two tentaculate larvae, but no stress is laid on its identification as such.

In comparing the Barrier Reef specimens with their nearest known relatives only the Krohn-stage can be used, since this stage alone was described in *T. sunieri* (Stiasny,

1921*b*, p. 101, figs. 1–4). The Barrier Reef specimen differs from *T. sunieri*, and agrees with *T. delsmanni* in size and proportions, in the greater number of tentacles, in the presence of inferior lateral ridges, each with a short tentacle-like process, and in the shape of the inferior dorsal groove. The proboscis-coelom in T. *sunieri* is broad and rounded ; it is not described in the corresponding stage of *T. delsmanni*. The apparent absence of a secondary circumanal ring in *T. delsmanni* cannot be stressed, since the material was admittedly not well preserved.

These specimens are therefore referred somewhat doubtfully to *T. delsmanni*. In any case they increase the probability of the distinctness of *T. delsmanni* and *T. sunieri*, of which Stiasny-Wijnhoff and Stiasny were not convinced.



Text-fig. 17.—Fragment of a tentaculate larva in Spengel stage. (× 40.) *ep.o.*, lateral epithelial organ.

No tentaculate larva with coelom close to gut has been traced to its adult. Stiasny-Wijnhoff and Stiasny (1927, p. 189) suggest that it may be the type characteristic of the genus *Spengelia*, of which six species have been described from the Indo-Pacific region.

12. *Tornaria* sp. ? (Text-fig. 18).

Regressive stage, probably of a tentaculate larva.

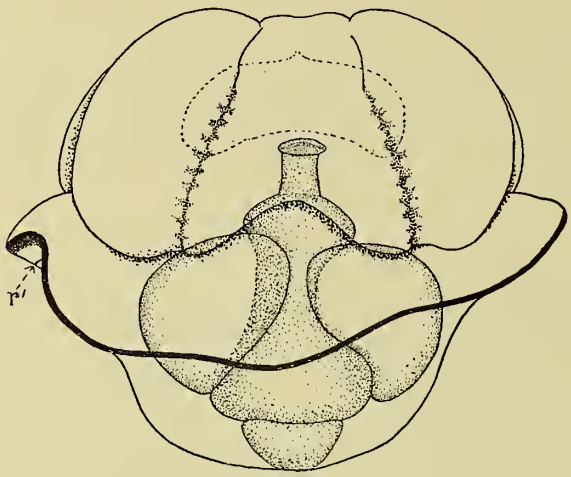
Height 2 mm. ; diameter $2\frac{1}{2}$ mm.

Body-wall almost opaque. Upper part of larva depressed, with apical pole invaginated ; axis of anal field about $\frac{1}{2}$ total height ; greatest diameter at level of ciliated ring.

Grooves of oral field narrow, overhung by the swollen ridges, on the borders of which no ciliated bands are visible. Praeoral field of anchor-shaped type. Oral arch low, wide. Inferior lateral groove a slight radial depression. Inferior dorsal groove, if present, merged in the general constriction of this zone. Tentacles reduced to almost imperceptible, low bosses ; approximate tentacle formula V. 9 to 11, 9 to 11 ; L. ? 4, ? 4 ; D. 8 to 10, 8 to 10. Circular ciliated band broad. A secondary, transparent circumanal ring within this, distant from it only a little more than width of ciliated band.

Proboscis-coelom well developed ; shape doubtful. A pair of large coelomic pouches close to gut. Collar-coelom ?. Stomach large, constricted by the coelomic pouches ; hind-gut small, conical.

A single specimen from Station 19 (16° 20′ S., 146° 3′ E.), taken 20th October, 1928, at 11.42 a.m. in the Nansen vertical net (180 metres of wire out).



TEXT-FIG. 18.—*Tornaria* in regressive stage. Ventral view. (× 30.) *r'*. Secondary circumanal ring.

It is impossible to relate this larva with certainty to any other. The position of the coelom and of the circumanal transparent ring suggest the tentaculate larvae referred to *T. delsmanni*, but the shape of the anal field and relative size of the diameter of the main ciliated ring are very different. The distance between the developmental stages represented makes comparison difficult, and if the tentaculate fragment from Station 35 is specifically identical with the younger specimens, the older larva is almost certainly distinct.

REFERENCES.

BOULENGER, G. A. 1910. Les Batraciens. Encyclopédie Scientifique, Paris, pp. 1–305.

—— and ANNANDALE, N. 1918. Rec. Ind. Mus. XV, pp. 51–67.

BOURNE, G. C. 1889. On a Tornaria found in British Seas. J. Marine Biol. Ass. (2) I, pp. 63–68, pls. vii, viii.

CALMAN, W. T. 1909. Crustacea, in Lankester's Treatise on Zoology, VII (3), pp. 1–346.

DAKIN, W. J. 1916. A New Species of Enteropneusta, *Ptychodera pelsarti*, from the Abrolhos Islands. J. Linn. Soc. Zool. London, XXXIII, pp. 85–100, pls. i, ii.

ESCHSCHOLTZ, FR. 1825. Oken's Isis, p. 740, pl. v, fig. 8.

GIARD, A. 1891. Sur le bourgeonnement des larves d'*Astellium spongiforme* Gd. et sur la Poecilogonie chez les Ascidies composées. Comptes Rendus de l'Ac. Sci., Paris, CXII, pp. 301–304.

—— 1892. Nouvelles Remarques sur la Poecilogonie. Comptes Rendus de l'Ac. Sci., Paris, CXIV, pp. 1549–1552.

GRAVIER, C. 1905. Sur le *Ptychodera erythraea* Spengel. Bull. Soc. Philom. Paris (sér. 2), VII, pp. 69–74, 4 figs.

HILL, J. P. 1897. The Enteropneusta of Funafuti. Mem. Austral. Mus. III, pp. 203–210, pl. ix.

HORST, C. J. VAN DER. 1924. West-indische Enteropneusten. Bijdr. tot de Dierkunde, XXIII, pp. 33–60, pls. iv–vii.

—— 1930. Papers from Dr. Mortensen's Pacific Expedition 1914–16 : LI, Observations on some Enteropneusta. Vidensk. Medd. naturh. Foren, Kjob. LXXXVII, pp. 135–200, figs. 1–64.

Klunzinger, C. B. 1902. Über *Ptychodera erythraea* Spengel aus dem Rothen Meere. Verh. Deutsch. Zool. Ges. XII, pp. 195–202, figs. 1–4.

MacBride, E. W. 1920. Larvae of Echinoderma and Enteropneusta. British Antarctic ("Terra Nova") Exped. 1910, Nat. Hist. Rep., Zool. London, IV (3), pp. 83–94, pls. i, ii.

Maser, O. 1913. Über *Balanoglossus carnosus* (Willey) und eine ihm nahestehende, neue Art von Neucaledonien. Zool. Jahrb. Abt. Anat. XXXIII, pp. 361–430, pls. xxv–xxix.

Menon, K. R. 1903. Enteropneusta from Madras. Quart. J. Micr. Sci., London, XLVII, pp. 123–131, pl. x.

Miyashita, Y. 1925. Über Tornaria-Larven aus Japanischen Küste. Dobutsugaka Zasshi, Tokyo, XXXVII, No. 438. [Not seen. Quoted from Stiasny, 1928.]

Morgan, T. H. 1894. The Development of *Balanoglossus*. J. Morph. IX, pp. 1–86, pls. i–vi.

Punnett, R. C. 1903. The Enteropneusta. In Gardiner, J. S., Fauna and Geog. Maldive and Laccadive Archipelagoes, II. pp. 631–680, pls. xxxvii–xlvi, Cambridge.

Ritter, W. E. 1894. On a new *Balanoglossus* Larva from the Coast of California, and its Possession of an Endostyle. Zool. Anz. XVII, pp. 24–30, figs. 1, 2.

—— and B. M. Davis. 1904. Studies on the Ecology, Morphology and Speciology of the Young of some Enteropneusta of Western North America. Univ. Calif. Publ. Zool. I (5), pp. 171–210, pls. xvii–xx.

Schmarda, L. K. 1871–2. Zoologie, I, p. 273 [Not seen. Quoted from Spengel, 1904*c*.]. 2nd edn. 1877, pp. 367–369, fig. 237.

Spengel, J. W. 1893. Fauna and Flora Neapel, XVIII, Enteropneusten, pp. xii, 756 [2], 36 pls. (col.), 1 map.

—— 1903. Neue Beiträge zur Kenntniss der Enteropneusten. 1. *Ptychodera flava* Eschscholtz, von Laysan. Zool. Jahrb. Abt. Anat. XVIII, pp. 271–326, pls. xxiv–xxix.

—— 1904*a*. Neue Beiträge . . . 2. *Ptychodera flava* von Funafuti. Zool. Jahrb. Abt. Syst. XX, pp. 1–18, pl. i, ii.

—— 1904*b*. Neue Beiträge . . . 4. *Ptychodera erythraea*. Zool. Jahrb. Abt. Syst. XX, pp. 413–428. figs. A, B.

—— 1904*c*. Eine wieder aufgefundene Enteropneusten-Art (*Balanoglossus tricollaris* Schmarda). Zool. Anz. XXVIII, pp. 52–54.

Stiasny, G. 1921*a*.* Über westindische Tornarien nebst einer Übersicht über die bisher bekannten tentaculaten Tornarien. Versl. gewone Akad. Amsterdam, XXIX (also in Proc. R. Acad. Amsterdam, XXIII, 1921, pp. 2–36, pls. i, ii, figs. 1–3).

—— 1921*b*. Eine neue Tornaria aus dem ostindischen Archipel (*Tornaria sunicri*). Zool. Meded. Leiden, VI, pp. 101–108, figs. 1–4.

—— 1922.* Die Tornarien-sammlung von Dr. Th. Mortensen. Vidensk. Medd. naturh. Foren. Kjob. LXXIII, pp. 123–137, figs. 1–9.

—— 1928. Tornarien von Japan. Zool. Jahrb. Abt. Syst. LVI, pp. 67–92, figs. 1–19.

Stiasny-Wijnhoff, G., and Stiasny, G. 1926. Über Tornarientypen und ihre Beziehung zur Systematik der Enteropneusten. Zool. Anz. LXVIII, Leipzig, pp. 159–165, figs. 1–9.

—— 1927. Die Tornarien. Kritik der Beschreibungen und Vergleich sämtlicher bekannter Enteropneusten-Larven. Ergebn. Fortschr. der Zool. VII, Jena, pp. 38–208, figs. 1–78, 7 charts.

Willey, A. 1897. On *Ptychodera flava* Eschscholtz. Quart. J. Micr. Sci. London, XL, pp. 165–183, pl. 5.

——— 1899. Enteropneusta from the South Pacific, with Notes on West Indian Species. Willey, A., Zoological Results, Part III, pp. 223–334, pls. xxvi–xxxii.

* These dates are taken from the wrappers of parts of the respective periodicals. They are each a year later than those quoted by Stiasny-Wijnhoff and Stiasny (1927), which may perhaps be the dates when the papers were read. 1921*a* has been seen by me in ' Proc. R. Acad. Amsterdam ' only.